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LATE HEMPHILLIAN CAT (MAMMALIA, FELIDAE) FROM THE BONE VALLEY FORMATION OF CENTRAL FLORIDA

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ABSTRACT—Dental and postcranial remains of a lynx-like cat are described from the latest Hemphillian Upper Bone Valley Formation of the central Florida phosphate mining district. This cat is referred to the species *Felis rexroadensis* based on numerous dental characters and size. The Bone Valley *F. rexroadensis* was larger than the present-day bobcat and smaller than the present-day puma. Forelimb functional anatomy, particularly in the degree of mediolateral rotation of the elbow joint, suggest that the Bone Valley *F. rexroadensis* was forest-adapted. This occurrence represents the oldest-known *Felis* in Florida and it adds to the poorly known fossil record of early *Felis* in North America.

INTRODUCTION

THE FOSSIL RECORD in North America of the present-day cat genus *Felis,* as recognized in the present study, spans at least the last five million years. The only reported occurrences of pre-Blancan (early Pliocene-early Pleistocene) *Felis* are from the late Hemphillian (latest Miocene-earliest Pliocene) of Oregon (Shotwell, 1956) and the Oklahoma panhandle (Savage, 1941), and a possible very early occurrence from the Valentinian (medial Miocene) of Colorado (Schultz and Martin, 1972). During the Blancan *Felis* has been reported from many localities in western North America, including the Oklahoma and Texas panhandles (Savage, 1960; Dalquest, 1975), the Rexroad Local Fauna of Kansas (Stephens, 1959), the San Pedro Valley of Arizona (Gazin, 1942), the Hagerman Local Fauna of Idaho (Gazin, 1933; Bjork, 1970), and the Ringold Local Fauna of Washington (Gustafson, 1978). Throughout the Pleistocene, *Felis* was a widespread element of North American mammalian faunas, as it also was in South America and the Old World. Previous studies of North American fossil *Felis* include, for example, Kurtén (1973) and Glass and Martin (1978).

There have been several studies of post-Hemphillian *Felis* of Florida. Kurtén (1965) reviewed the "Pleistocene" (Blancan-Rancholabrean) Felidae of Florida. Gillette (1976) described a new species of late Pleistocene *Felis* from Florida. There are no previous studies of *Felis* from the rich late Hemphillian mammalian fauna of the Upper Bone Valley Formation of central Florida. The purpose of this report is to describe a sample of *Felis rexroadensis* from the Upper Bone Valley of Florida and to discuss the significance of this occurrence.

The taxonomy of extant felids is controversial. Some workers choose to include all present-day species except *Acinonyx,* the cheetah, in the genus *Felis.* Other workers split the same species into numerous subgenera or genera. As it is beyond the scope of this paper to address this problem, we follow Simpson's (1945) use of the genus *Felis.*

The following institutional abbreviations are used in the text: F:AM, Frick American Mammals, The American Museum of Natural History, New York; UF, Vertebrate Paleontology Collection, Florida State Museum, University of Florida, Gainesville; TRO, Timberlane Research Organization, Lake Wales, Florida; UKMNH, University of Kansas Museum of Natural History; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; and USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order CARNIVORA Bowdich, 1821
Family FELIDAE Gray, 1821
FELIS REXROADENSIS Stephens, 1959
Text-figs. 1–8

Type specimen and locality.—UMMP 34195, partial skull with incisors, P^3 and P^4, alveoli for C and M^1, from Rexroad Local Fauna,

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TABLE 1—Dental measurements (mm) for *Felis rexroadensis* from the late Hemphillian Upper Bone Valley Formation of Florida.

	TRO 1551	TRO 1550	TRO 1450	UF 24402
AP[1] length P^4	17.7	17.9	—	—
T[2] width P^4	8.9	8.9	—	—
AP length P_3	—	—	9.8	—
T width P_3	—	—	5.1	—
AP length P_4	—	—	13.0	12.3
T width P_4	—	—	6.5	5.8
AP length M_1	—	—	—	15.2
AP width M_1	—	—	—	6.6

[1] Greatest anteroposterior.
[2] Greatest transverse.

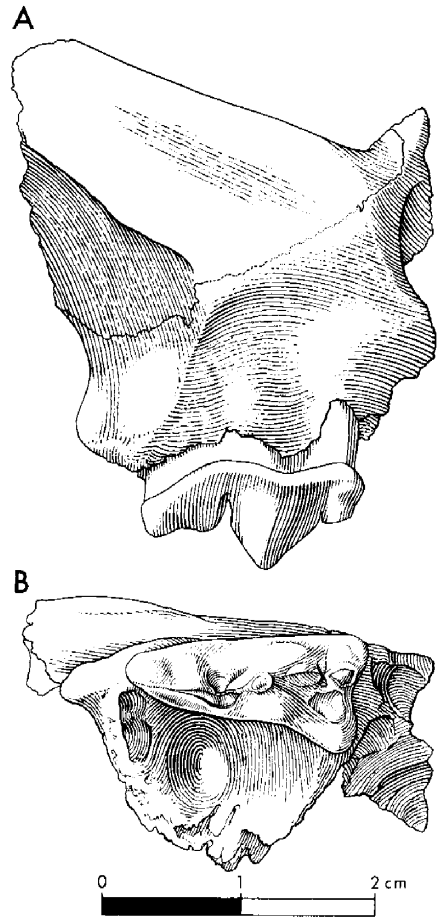
Rexroad Formation, early Blancan, Meade County, Kansas (Stephens, 1959).

Referred material from Florida.—TRO 1551, skull fragment with parts of the right maxillary and jugal bones, anterior part of zygomatic arch, P^4, alveolus of M^1; TRO 1550, left P^4; TRO 1450, right ramus with P_3–P_4; UF 24402, left ramus with P_4–M_1; TRO 1552, partial left M_2; TRO 1444, distal fragment right humerus; TRO 1442, 1443, distal fragments left humeri; TRO 1446, right proximal ulna with olecranon process; TRO 1449, left proximal ulna with olecranon process; TRO 1445, right calcaneum; TRO 1447, left metacarpal IV; TRO 1447, distal fragment metapodial.

Geographic and stratigraphic location.—Bone Valley District of central Florida, Polk County. These occurrences are from the Upper Bone Valley Formation which, based on associated *in situ* vertebrate fossils, is latest Hemphillian (latest Miocene or earliest Pliocene) in age.

Because of the nature of the open-pit phosphate mining operations in the Bone Valley District, in many cases the exact stratigraphic provenance of fossil specimens collected from mining spoil piles ("wells") is unknown. In other cases specimens are collected *in situ* in the pits. Of the specimens discussed here, only UF 24402 and TRO 1550 were collected *in situ* from the late Hemphillian Upper Bone Valley Formation; the others were collected from spoil piles. However, there is no reason to suspect that all specimens described in this report are not of latest Hemphillian age.

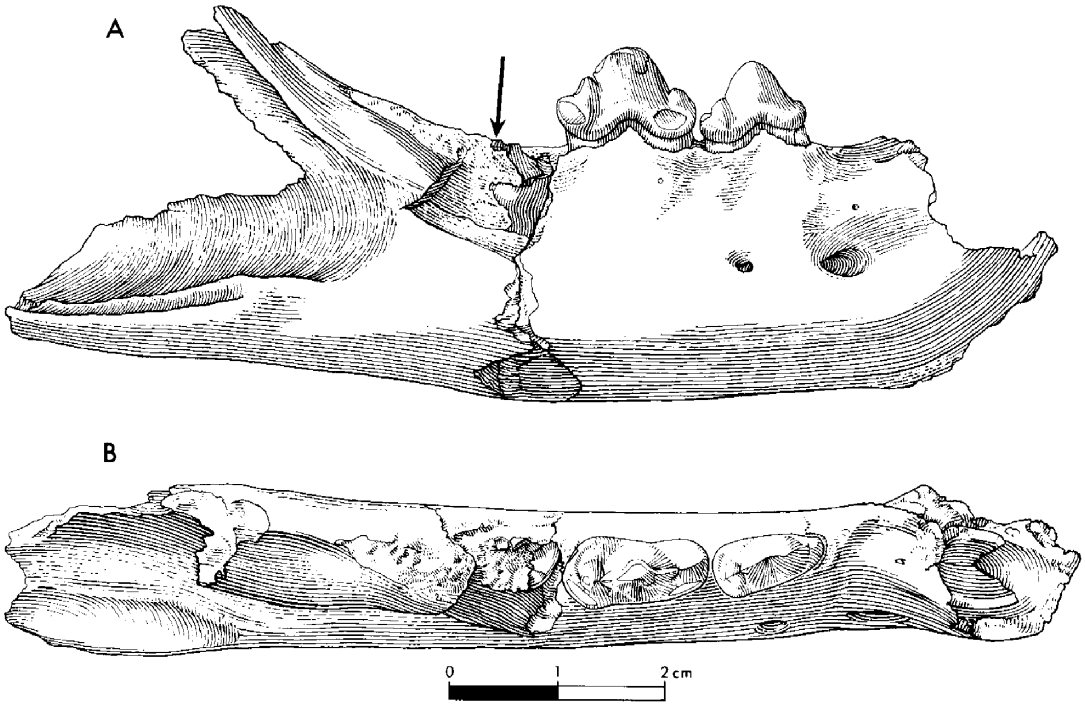
Diagnosis.—In the original description of



TEXT-FIG. 1—Skull fragment with right P^4 of *Felis rexroadensis*, TRO 1551, from Palmetto mine Upper Bone Valley, Polk County, central Florida. *A*, Lateral view. *B*, Occlusal view.

Felis rexroadensis, which was based only on portions of the skull and associated upper dentitions, Stephens (1959, p. 41) presented the following diagnosis: "A *Felis* smaller than *F. lacustris* Gazin. Differentiated from Recent cats in having a petrosal bone with expanded anterior border; from an undescribed petrosal of *F. lacustris* (UKMNH 4664) from the Rexroad local fauna, Locality 2A, in being smaller and having a more complicated surface. The form differs from *F. peii* [Teilhard de] Chardin [and Leroy] (1945), of which the petrosal is unknown, in having a narrower palatal width across the distal extremities of the P^4."

Based on a re-examination of the topotypic



TEXT-FIG. 2—Right ramus of *Felis rexroadensis*, TRO 1450, from the Palmetto Mine Upper Bone Valley Formation, Polk County, central Florida. *A*, Lateral view with P_3, P_4, and alveolus for M_1 filled with secondarily deposited bone (arrow, see text). *B*, Occlusal view.

material from the Rexroad Local Fauna and the Upper Bone Valley specimens, the following suite of characters also differentiate *F. rexroadensis* from other taxa: loss of P^1 and P_2, crown height of P_3 shorter than that of P_4, reduction of talonid on M_1, laterally compressed premolar-molar series, reduction in protocone of P^4, relatively robust ramus (particularly at symphysis), and retention of reduced talonid on M_1. Size larger than *F. proterolyncis* (Savage, 1941), *F.* (*Lynx*) *stouti* (Schultz and Martin, 1972), the bobcat *F.* (*Lynx*) *rufus* and the domestic cat *F. catus*; smaller than *F. lacustris* (Gazin, 1933, 1942), *F. studeri* (Savage, 1960), and the extant species *F. concolor,* and *F. leo.*

Description.—The Bone Valley cat *Felis rexroadensis* is similar in size to the topotypic material of this species from the Rexroad Local Fauna (Table 1 and Stephens, 1959). These specimens are medium-sized relative to other fossil and extant species of *Felis* (see Diagnosis).

A skull fragment, TRO 1551 (Text-fig. 1), includes the anterior portion of the zygomatic arch and the infraorbital canal. Anteriorly, the maxillary-jugal suture lies posterior to the anterior opening of the infraorbital canal and extends posteriorly to a position above the alveolus for M^1. Ventral to the zygomatic arch on the jugal and maxillary, there is a well developed scar and anterior ridge, which outlines the anterior extent of the origin of the masseter.

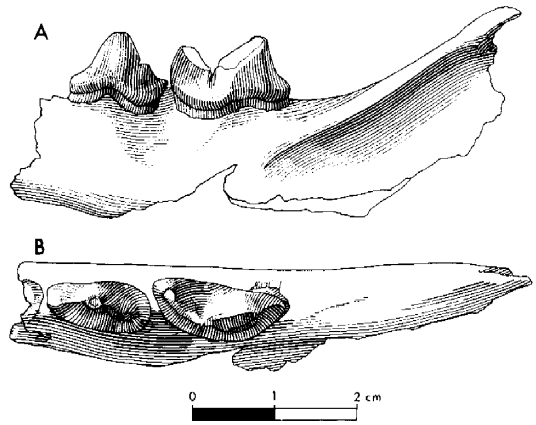
The upper carnassial, P^4, is represented by two specimens, TRO 1550 and 1551. This tooth is triangular in occlusal cross-section with the greatest width developed anteriorly. As is characteristic of *Felis,* the protocone is reduced and it is much smaller than the parastyle. A crest, the paracrista, extends from just posterior to the parastyle to the paracone. The paracone, the tallest cusp of P^4, forms the anterior part of the carnassial shear. The carnassial notch between the paracone and metacone is, as in other *Felis,* relatively deep. In contrast to other feloids such as the pseudaelurines, the height of both upper and lower

carnassials is reduced. The M^1 is not represented by any specimens, but in TRO 1551 the characteristically small alveolus is preserved. It appears that the M^1 was double-rooted, although the bony separation between the root alveoli is weakly developed.

The ramus of *F. rexroadensis* from the Upper Bone Valley is represented by two specimens, TRO 1450 and UF 24402 (Text-figs. 2 and 3). The ramus is more robust than in advanced *Felis*. The symphysial region is particularly robust with an alveolus for a large canine. The postcanine diastema is shortened as in other *Felis*, and in contrast to more primitive feloids such as pseudaelurines, both the P_1 and P_2 are absent. In TRO 1450 there are two prominent mental foramina, a large and deep anterior one that lies below the postcanine diastema and a small and shallow one that lies below the posterior portion of P_3. Two additional extremely small and shallow foramina lie ventral to the postcanine diastema. In TRO 1450 the depth of the ramus anterior to P_3 is 23.0 mm and the transverse width is 10.5 mm. Below the posterior accessory cusp of P_4, the depth of the ramus is 23.0 mm and the transverse width is 11.0 mm. These measurements are larger than those given for rami of *F. proterolyncis* from the late Hemphillian of the Oklahoma panhandle (Savage, 1941, p. 699).

A deep masseteric fossa is developed labially on the ascending and posteroventral parts of the ramus in TRO 1450. Lingually, there is a mandibular foramen on the posteroventral part of the ramus. The premolars and molars are "crowded," i.e., they are slightly rotated internally. As evidenced by the large alveolus and root fragment in TRO 1450, the canine was relatively robust. The premolars and molars are more laterally compressed, which is similar to other species of *Felis*, and advanced relative to other feloids such as pseudaelurines.

The P_3 is the smallest tooth of the cheek tooth series. In *F. rexroadensis*, the crown height of the P_3 is less than that of P_4. This reduction is characteristic of *Felis* and advanced over the character state seen in many pseudaelurines where the P_3 is not significantly lower in crown height than the P_4. P_3 has a small anterior cusplet (paraconid of some workers), a large principal cusp (protoconid), a small posterior cusplet (metaconid), and a rudimentary posteromost cusplet (talonid) developed on a weak posterior cingulum.

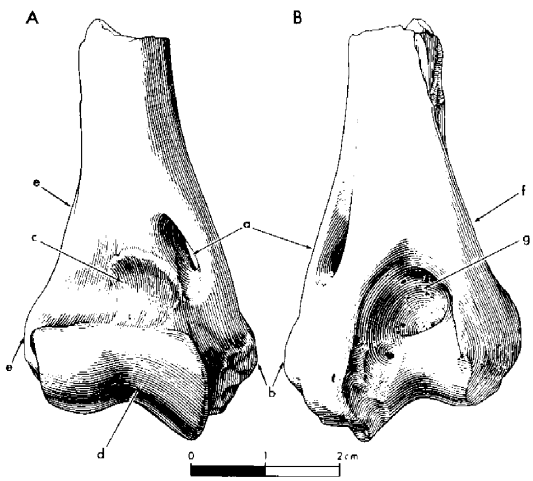


TEXT-FIG. 3—Left ramus of *Felis rexroadensis*, UF 24402, from the Payne Creek Mine, TRO Quarry, Upper Bone Valley Formation, Polk County, central Florida. *A*, Lateral view with P_4 and M_1. *B*, Occlusal view.

The P_4 of TRO 1450 and UF 24402 is larger than the P_3 of TRO 1450, and anteroposterior arrangements of cuspids are similar, except that in UF 24402 the posteromost cusplet is absent. In the M_1 the anterior part of the carnassial, the paraconid, is smaller than the posterior part of the carnassial, the protoconid. In UF 24402, the talonid, or posterior cingulum, is relatively well developed in *F. rexroadensis* in contrast to numerous extant species of *Felis*, but the talonid is reduced in contrast to that of pseudaelurines. There is a dental pathology developed in TRO 1540 (Text-fig. 2). During the life of this individual the M_1 was broken off at the base of the crown leaving the roots in their alveoli. There was subsequent deposition of bone that completely covered the posterior root and partially covered the anterior root.

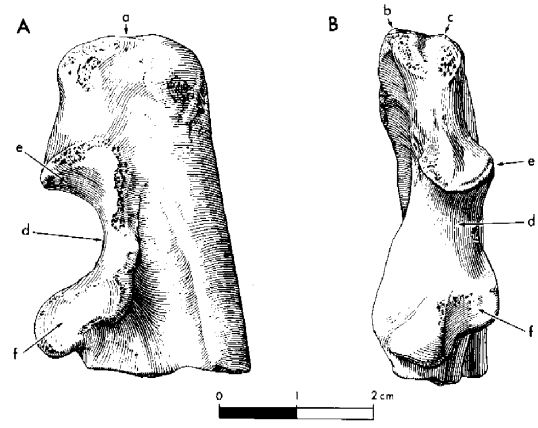
The postcranial elements described below from the Bone Valley are referred to *Felis rexroadensis* because they are of the appropriate size relative to the dentitions and there is no other cat of similar size known from these sediments.

Three distal humeri are represented by TRO 1442 (Text-fig. 4), TRO 1443 (both right), and TRO 1444 (left). In general morphology these are characteristic of *Felis* as described below (also see Discussion). In anterior aspect and medially there is a prominent su-

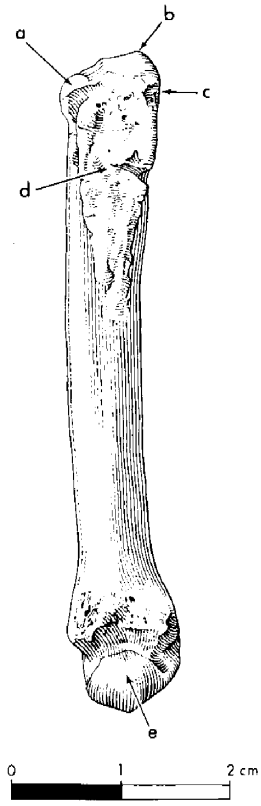


TEXT-FIG. *4*—Distal right humerus of *Felis rexroadensis,* TRO 1442, from the Upper Bone Valley Formation, Polk County, central Florida. *A,* Anterior aspect. *B,* Posterior aspect. a, supracondylar foramen; b, medial epicondyle; c, coronoid fossa; d, trochlea; e, lateral epicondyle; f, supracondylar ridge; g, olecranon fossa.

pracondylar foramen proximal to the medial epicondyle of the trochlea. Proximal to the trochlea, on the anterior face, there is a distinct coronoid fossa. The lateral epicondyle is continuous with the supracondylar ridge.



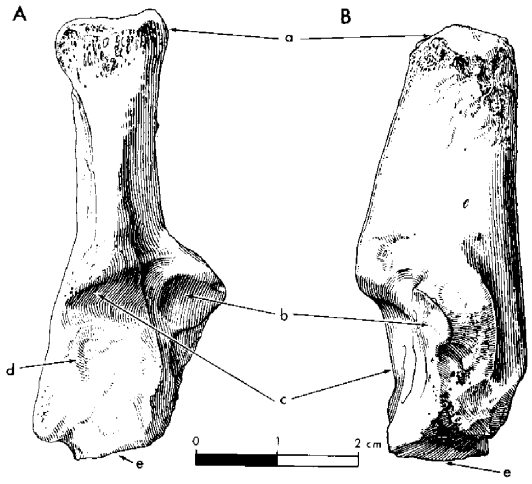
TEXT-FIG. *5*—Proximal left ulna of *Felis rexroadensis,* TRO 1446, from the Upper Bone Valley Formation, Polk County, central Florida. *A,* Lateral view. *B,* Dorsal view. a, olecranon process; b, medial tuberosity; c, lateral tuberosity; d, semilunar notch; e, coronoid process; f, radial notch.



TEXT-FIG. *6*—Dorsal view of left metacarpal IV of *Felis rexroadensis,* TRO 1447, from the Upper Bone Valley Formation, Polk County, central Florida. a, facet for articulation with metacarpal III; b, unciform facet; c, articular area for metacarpal V; d, area of arthritic lipping; e, distal articular head.

Proximal to the trochlea on the posterior surface, there is a deep olecranon fossa that limits rotation of the ulna. The olecranon fossa is well inclined relative to the longitudinal axis of the humerus. The inclination is similar to such carnivores as the wolverine, *Gulo luscus,* and the jaguar, *Felis (Panthera) onca,* and different from that of the dog, *Canis familiaris,* and the cheetah, *Acinonyx jubatus* (see Gonyea, 1978). The functional implications of the inclination of the olecranon fossa in *F. rexroadensis* as represented by the Florida sample will be presented in the "Discussion" section below.

Two proximal ulnae are represented by TRO 1449 (right) and TRO 1446 (left). The olecranon process is robust (Text-fig. 5). On



TEXT-FIG. 7—Dorsal view of right calcaneum of *Felis rexroadensis*, TRO 1445, from the Upper Bone Valley Formation, Polk County, central Florida. a, proximal tuber; b, medial astragalar facet; c, lateral astragalar facet; d, weak groove for attachment of annular ligament; e, cuboid facet.

this process the medial tuberosity is more robust than the lateral tuberosity. The medial tuberosity is continuous with a prominent ridge for insertion of the triceps muscles. The semilunar, or trochlear, notch (greater sigmoid cavity) is inclined from the longitudinal axis of the shaft of the ulna. A distinct coronoid process is developed on the semilunar notch. The radial notch (lesser sigmoid cavity) lies lateral to the coronoid process.

The left metacarpal IV is represented by TRO 1447 (Text-fig. 6). On the proximal articular surface is a small facet for articulation with metacarpal III. Lateral to this metacarpal III facet, and separated from it by a groove, is a large convex unciform facet, which occupies much of the proximal surface. Lateral to the unciform facet is a flattened ridge and crescentic pit for articulation with metacarpal V. Distal to this pit is a roughened surface for attachment of ligaments. Just distal to the proximal articular surface on the dorsal surface there is an area of arthritic lipping. On the distal articular head of the metacarpal IV the sagittal ridge is well-developed ventrally but becomes faint and is absent dorsally.

The right calcaneum is represented by TRO 1445 (Text-fig. 7). On the proximal extremity (or tuber) is a medial tuberosity, a concave area for attachment of the Achilles tendon, and a lateral tuberosity. On the dorsal surface are medial and lateral facets for articulation with the astragalus, but these are not as distinct or as continuous distally as in some other *Felis*. Distal to the lateral astragalar facets is a weak groove for attachment of the annular ligament. On the distal-most extremity is a prominent cuboid facet.

DISCUSSION

Relationships.—The Upper Bone Valley cat *Felis rexroadensis* has characters that are derived relative to those of pseudaelurines, and primitive relative to those of other species of the genus *Felis*. The derived characters include: loss of P^1 and P_2, crown height of P_3 shorter than that of P_4, reduction of talonid on M_1, laterally compressed premolar-molar series, reduction in protocone of P^4. Primitive *Felis* characters include: anteriorly placed protocone in P^4, relatively robust ramus (particularly at symphysis), and retention of reduced talonid on M_1 (which is absent in more derived *Felis*). This array of characters make the Florida cat similar to the fossil species *F. proterolyncis, F. rexroadensis,* and *F. lacustris*. During the present study, the Upper Bone Valley *Felis* was compared to the original type series in the UMMP collection of *F. rexroadensis* from the Rexroad Local Fauna of Kansas (Stephens, 1959) and the USNM collection of *F. lacustris* from the Hagerman Local Fauna of Idaho (Gazin, 1933). In qualitative characters the Florida cat is similar to these two species and *F. proterolyncis* (Savage, 1941). However, there are significant differences in size that separate these three species of *Felis*. Based on this character, the Florida cat is indistinguishable from *F. rexroadensis* from Kansas. In summary the Florida cat is assigned to *F. rexroadensis* based on a similar stage of evolution as represented by size relative to the type series of this species from Kansas.

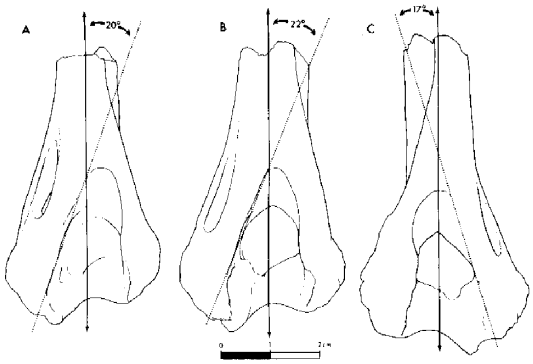
As has been stated in the literature, the fossil species discussed in this report are near the split of the superspecific groups of *Felis*. In relation to extant *Felis,* Glass and Martin (1978) stated that *Felis rexroadensis* is lynx-like in characters, including the small and rounded upper canines and large P^3 (no upper canines are known for Florida *F. rexroaden-*

sis). Paleontologists such as Kurtén (1968) and Glass and Martin (1978) have stated that the lynxes were of New World origin and subsequently dispersed to the Old World during the Villafranchian (Pliocene) at which time they were represented by the widespread species *F. (Lynx) issodorensis*. In this context, the early lynx-like *Felis stouti* described by Schultz and Martin (1972) is central to discussions of the New World origin of the lynxes. However, *Felis stouti* has numerous characters that suggest a close relationship to some member of the pseudaelurine complex rather than to the genus *Felis* (including *Lynx*). These primitive characters include retention of the P^1 and P^2, P_3 and P_4 about equal in size, and well-developed talonid on M_1. In addition, it is curious that there is a very early lynx species, *F. (Lynx) stouti,* in North America during the Valentinian (medial Miocene), and then a time gap of some 10 million years until the late Hemphillian when other lynx-like cats are represented at several North American localities, such as *F. proterolyncis* from Oklahoma (Savage, 1941), *F. rexroadensis* from Oregon (Shotwell, 1956, *fide* Stephens, 1959), and *F. rexroadensis* from Florida.

During the present study some interesting similarities have come to light regarding the problem of the origin of lynx-like *Felis*. In the F:AM collection there is a large and undescribed collection of Turolian *Felis* from China. Using the existing nomenclature, this sample would be referred to *Felis attica* (Teilhard de Chardin and Leroy, 1945; de Beaumont, 1961). *Felis attica* is very similar to the primitive lynx-like species *F. proterolyncis,* Florida *F. rexroadensis,* and *F. rexroadensis* from Kansas in characters such as loss of P_2, reduction of P^2, reduction of the crown height of P_3, reduction of the talonid on M_1, reduced protocone on P^4, and laterally compressed premolar-molar series. In addition, *Felis attica* is relatively small and it is similar in size to species such as *F. proterolyncis* and *F. (Lynx) rufus*. Based on these characters, it is possible that *F. attica* is close to the origin of lynxes. These similarities suggest that, in contrast to the hypotheses of Kurtén (1968) and Glass and Martin (1978), lynxes had an Old World origin during the Turolian and subsequently dispersed into North America during the late Hemphillian.

Biochronology.—The Florida cat is nearest in stage of evolution to the early Blancan *F. rexroadensis* from Kansas and more advanced than the late Hemphillian *F. proterolyncis* from Oklahoma. The Upper Bone Valley Formation and its vertebrate fauna have been traditionally thought to be late Hemphillian, i.e., roughly equivalent to the Coffee Ranch Local Fauna of the Texas panhandle. Recent work in progress based on other taxa of the Upper Bone Valley Fauna suggests a very latest Hemphillian biochron or perhaps even that this assemblage approximates the Hemphillian-Blancan boundary. For example, the *Dinohippus* sp. and *Nannippus minor* from the Upper Bone Valley Formation represent an advanced stage of evolution relative to horses at Hemphillian localities from the midcontinent (MacFadden, pers. observ.). Undescribed material of a Bone Valley sabertoothed cat is similar to *Smilodon* cf. *S. gracilis* from several Blancan localities in Florida (Webb, 1974; Webb, pers. comm., 1980). Therefore, it is not surprizing that the Upper Bone Valley *Felis* described here is most similar to the early Blancan *F. rexroadensis* from Kansas and this occurrence further suggests a young age (i.e., latest Hemphillian or Hemphillian-Blancan transition) for the Upper Bone Valley Formation of central Florida.

Functional interpretations.—Gonyea (1976a, 1976b, 1978) presented a series of functional and ecological studies of cats and other carnivores that can be applied to the Upper Bone Valley *Felis rexroadensis*. Gonyea showed that the inclination of the olecranon fossa of the humerus and semilunar notch of the ulna relative to the longitudinal axis of these bones varies significantly in different cats. Some cats, such as the cheetah, *Acinonyx jubatus,* and other carnivores, such as the domestic dog, *Canis familiaris,* have relatively low (about 0°–3°) inclinations of the humeroulnar joint. Other cats and carnivores, such as the margay, *Felis wiedii,* and the wolverine, *Gulo luscus,* have relatively high (about 11°–15°) inclinations of the humeroulnar joint. These differences in inclination are correlated with habitat preference. Carnivores with low inclinations of this joint are relatively restricted in forelimb rotation in the mediolateral plane, and they are highly cursorial open-country adapted. Carnivores with high incli-



TEXT-FIG. 8—Outline drawings of posterior aspect of three distal humeri of *Felis rexroadensis* from the Upper Bone Valley Formation, Polk County, central Florida showing inclination of medial margin of olecranon fossa. See text and Gonyea (1976) for discussion of functional significance. *A*, TRO 1442, right; *B*, TRO 1443, right; *C*, TRO 1444, left.

nations of this joint are not as restricted in mediolateral movement of the forelimb and are hypothesized to be forest adapted. Gonyea's (1978) hypotheses based on osteological and anatomical characters were substantiated by known habitat preferences of extant felids and other carnivores.

Outline drawings of three humeri of Upper Bone Valley *Felis rexroadensis* that show the inclination of the olecranon fossa are presented in Text-fig. 8. The inclinations as measured from this illustration are 20°, 22°, and 17° (these are probably accurate to ±5° depending upon determination of longitudinal axis of these bones relative to the line drawn to limit the olecranon fossa). In comparison to Gonyea's (1978, in particular see fig. 1) measurements for numerous felids, the angle of inclination of the Upper Bone Valley *F. rexroadensis* is high, implying a forest-adapted animal. This interpretation based on functional morphology is corroborated by associated Bone Valley mammalian taxa which include numerous browsing or somewhat forest-adapted (as interpreted from dentitions) forms, such as rhinoceroses, tapirs, and peccaries.

Summary.—This report records the presence of a lynx-like cat, *Felis rexroadensis*, in the latest Hemphillian Upper Bone Valley Formation of central Florida, which is an early occurrence for this genus in North America. The assignment of the Florida cat to *F. rexroadensis*, which was previously known from the early Blancan of Kansas, suggests a latest Hemphillian or perhaps transitional Hemphillian-Blancan age for the Upper Bone Valley Formation of the central Florida phosphate mining district. Functional morphology of the forelimb implies that *F. rexroadensis* from Florida was apparently forest-adapted.

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REFERENCES

Beaumont, G. de. 1961. Recherches sur *Felis attica* Wagner du Pontian eurasiatique avec quelques observations sur les genres *Pseudaelurus* Gervais et *Proailurus* Filhol. Nouv. Arch. Mus. Hist. Nat., Lyon 6:17–45.

Bjork, P. R. 1970. The Carnivora of the Hagerman Local Fauna (late Pliocene) of southwestern Idaho. Am. Phil. Soc. Trans. 60:1–54.

Bowdich, T. E. 1821. An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travellers. J. Smith, Paris, 146 p.

Dalquest, W. W. 1975. Vertebrate fossils from the Blanco Local Fauna of Texas. Occas. Pap. Mus. Texas Tech. Univ. 3:1–52.

Gazin, C. L. 1933. New felids from the Upper Pliocene of Idaho. J. Mammal. 14:251–256.

——. 1942. The late Cenozoic vertebrate faunas from the San Pedro Valley, Arizona. U.S. Nat. Mus. Proc. 92:475–518.

Gillette, D. D. 1976. A new species of small cat from the late Quaternary of southeastern United States. J. Mammal. 57:664–676.

Glass, G. E. and L. D. Martin. 1978. A multivariate comparison of some extant and fossil Felidae. Carnivore 1:80–87.

Gonyea, W. J. 1976a. Behavioral implications of saber-toothed felid morphology. Paleobiology 2:332–342.

——. 1976b. Adaptive differences in the body proportions of large felids. Acta Anat. 96:81–96.

——. 1978. Functional implications of felid forelimb anatomy. Acta Anat. 102:111–121.

Gray, J. E. 1821. On the natural arrangement of vertebrose animals. Lond. Med. Repos. Rev. 15:296–310.

Gustafson, E. P. 1978. The vertebrate faunas of the Pliocene Ringold Formation, south-central Washington. Univ. Oregon Mus. Nat. Hist. Bull. 23:1–62.

Kurtén, B. 1965. The Pleistocene Felidae of Florida. Bull. Fla. State Mus., Biol. Sci. 9:215–273.

——. 1968. Pleistocene Mammals of Europe. Weidenfeld and Nicolson, Lond., 317 p.

——. 1973. Pleistocene jaguars in North America. Commentat. Biol. Soc. Sci. Fennica 62:1–23.

——. 1976. Fossil puma (Mammalia: Felidae) in North America. Neth. J. Zool. 26:502–534.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus differentiis synonymis locis. Editia decima, reformata. Vol. 1, Laurentii Salvii, Stockholm, 824 p.

Repenning, C. 1967. Palearctic-Nearctic mammalian dispersal in the late Cenozoic, p. 288–311 *In*: D. M. Hopkins (ed.), The Bering Land Bridge, Stanford Univ. Press, Stanford.

Savage, D. E. 1941. Two new middle Pliocene carnivores from Oklahoma with notes on the Optima Fauna. Am. Mid. Nat. 25:692–710.

——. 1960. A survey of various late Cenozoic vertebrate faunas of the Panhandle of Texas. Univ. Calif. Publ. Dept. Geol. Sci. Bull. 36:317–344.

Schultz, C. B. and L. D. Martin. 1972. Two lynx-like cats from the Pliocene and Pleistocene. Univ. Nebr. State Mus. Bull. 9:197–203.

Shotwell, J. A. 1956. Hemphillian mammalian assemblage from northeastern Oregon. Geol. Soc. Am. Bull. 67:717–738.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Am. Mus. Nat. Hist. Bull. 85:1–350.

Stephens, J. J. 1959. A new Pliocene cat from Kansas. Mich. Acad. Sci., Arts, Lett., Pap. 44:41–46.

Teilhard de Chardin, P. T. and P. Leroy. 1945. Les félidés de Chine. Publ. Inst. Geobiol. 11:1–58.

Webb, S. D. 1974. Pleistocene Mammals of Florida. Univ. Presses Florida, Gainesville, 270 p.

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